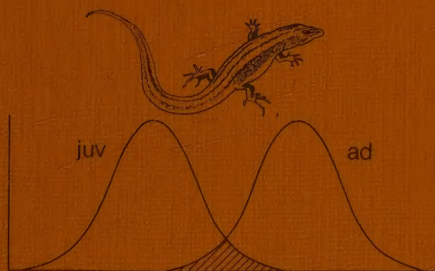


Competition and differences in niches and morphology between individuals, sexes and age classes in animal populations, with special reference to passerine birds

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COMPETITION AND DIFFERENCES IN NICHES AND MORPHOLOGY BETWEEN

INDIVIDUALS, SEXES AND AGE CLASSES IN ANIMAL POPULATIONS,

WITH SPECIAL REFERENCE TO PASSERINE BIRDS

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FK, Ög

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ABSTRACT

Size patterns in willow warblers on islands in a South Swedish lake and the nearby mainland were investigated. Individuals with territories on the mainland were larger than those on the islands. Food abundance was higher in the mainland territories, suggesting that these were preferred. Large warblers probably had a competitive advantage over smaller ones and thereby prevented them from establishing territories on the mainland.

The effect of interspecific competition on habitat utilization in the chaffinch was studied on islands in a lake and the nearby mainland. On the islands, where there were few competing species, there were significant differences between the males and the females in habitat utilization, while this was not the case on the mainland.

A study of sexual size dimorphism in the great tit in relation to the number of competing congeners was carried out in coniferous plantations in southernmost Sweden. Sexual size dimorphism in characters related to foraging was most pronounced in the plantations where the great tit coexisted with few competing congeners. The dimorphism is probably an adaptation for ecological displacement between the sexes to reduce intrapair competition.

A concept of the niche of a population that takes differences in resource utilization between age classes/life stages into account is proposed in a theoretical study. An examination of how competition between age classes, as reflected by niche overlap, affects the stability of equilibrium abundances is undertaken. This is done in a discrete-time model, where both reproduction and survival are frequency and density dependent. It is shown that increased competition sometimes has a stabilizing effect, in that it reduces the time lag effects inherent in the discrete-time model. Suggestions are made on how to extend the theory to cover situations where birth and death processes occur continuously and where the niche position of an individual depends on its size.



LIST OF PAPERS

This thesis is based on the following papers, which will be referred to by their Roman numerals.

- I Ebenman, B. and Nilsson, S.G. 1981. Size patterns in willow warblers *Phylloscopus trochilus* on islands in a South Swedish lake and the nearby mainland. - *Ibis* 123: 528-534.
- II Ebenman, B. and Nilsson, S.G. 1982. Components of niche width in a territorial bird species: Habitat utilization in males and females of the chaffinch (*Fringilla coelebs*) on islands and mainland. - *Amer. Natur.* 119: 331-344.
- III Ebenman, B. Sexual size dimorphism in the great tit (*Parus major*) in relation to the number of coexisting congeners. - Manuscript.
- IV Ebenman, B. Niche differences between age classes and intra-specific competition in age-structured populations. - Manuscript.

TACK

Drivkraften bakom det arbete som lett fram till denna avhandling är ett stort intresse för naturen i allmänhet och för fåglar i synnerhet. Det är därför naturligt att huvuddelen av uppsatserna behandlar fåglarnas ekologi. Det är dock min förhoppning att de även kan vara av ett visst allmängiltigt ekologiskt intresse. Uppsatserna bygger till största delen på fältstudier. Den sista uppsatsen, som behandlar nischskillnader mellan olika åldersklasser i en population, grundar sig dock inte på studier utförda i fält. Här har jag istället utgått från en matematisk modell. En del ekologer är skeptiska mot användandet av matematiska modeller, då de menar att sådana modeller representerar en alltför förenklad bild av verkligheten. De förordar istället noggrannt utförda fältstudier. Jag tycker dock inte att det föreligger något generellt motsatsförhållande mellan dessa metoder så länge de ledsagas av biologiskt intressanta frågeställningar. Båda metoderna är värdefulla och kompletterar varandra.

De första åren av min utbildning hade jag nöjet att ha Staffan Ulfstrand som handledare. Jag vill varmt tacka honom för all hjälp under dessa år. Jag är också tacksam för den hjälp jag fått av Per Brinck, zoologiska avdelningens chef, under slutet av min utbildning. Hans genomgång av mina manuskript har varit värdefull och lett till förbättringar i deras innehåll. Under arbetets gång och vid utformningen av de olika uppsatserna har jag också haft stor nytta av goda råd från mina vänner i fågelgruppen. Jag vill speciellt tacka Sigfrid Lundberg för många trevliga och stimulerande pratstunder.

Astrid Ulfstrand och Steffi Douwes har med stor skicklighet framställt samtliga figurer. Astrid har också tecknat omslagsfiguren, som illustrerar nischskillnader mellan olika individer i en population. Anne Odham renskrev manuskripten och Gunilla Lindquist utförde slutredigeringen. Ett varmt tack till er alla.

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BACKGROUND AND SUMMARY OF RESULTS

Many ecologists, including myself, hold the view that competition among and within species for limited resources plays an important role in structuring ecological communities. This is not a new idea. Already Darwin emphasized the importance of competition, and considered it to be of greater influence on the distribution of species than any other component of the environment. He also proposed that character divergence between species and between individuals within species was a way of reducing competition (The origin of species, pp. 155-169). This emphasis on competition experienced a renaissance with the works of David Lack (1947) and Robert MacArthur (1958) on birds. Contemporary ecologists have shown that species communities often exhibit regular patterns as regards species co-occurrences, size differences between species coexisting within habitats and species/genus ratios. These patterns are highly compatible with explanations invoking competition (see Grant 1968, 1981, Abbott et al. 1977, Diamond 1975, Faaborg 1982 for studies on birds; Schoener 1977, Roughgarden 1979 for lizards; Bowers and Brown 1982 for rodents; Gatz 1981 for fishes; and Price 1975, Pearson and Mury 1979 for insects).

In recent years there has been a controversy about the causes of these patterns. Some authors claim that the characteristics of coexisting species cannot be distinguished from random patterns generated by so-called null models, and that it is therefore no need to invoke competition (Simberloff 1978, Connor and Simberloff 1978, 1979, Strong et al. 1979, Simberloff and Boecklen 1981). The methods used by these authors to generate random distributions against which to test the real data have been subjected to severe criticism (Grant and Abbott 1980, Wright and Biehl 1981, Hendrickson 1981, Diamond and Gilpin 1982, Thomas and Foin 1982, Alatalo 1982). The major problems with the procedure of Simberloff and colleagues are: (a) dilution of competitive effects by drawing random samples from a whole species pool rather than from ecologically defined guilds where there is a priori reason to believe that species compete; (b) dependence between the real data and the randomly generated distributions; and (c) use of weak and inappropriate statistical tests (Grant and Abbott 1980, Diamond and Gilpin 1982). All this consistently favours the acceptance of the null hypothesis of no competition.

In fact it is almost impossible to reject the null hypothesis even if false. Comparisons of observed patterns with appropriate random distributions reject the null hypothesis of no competition (Grant and Abbott 1980, Wright and Biehl 1981, Gilpin and Diamond 1982, Bowers and Brown 1982). In balance, observed patterns of species communities are often highly consistent with explanations invoking competition between species for limited resources.

The studies referred to above have mostly been concerned with the effects of competition on the "average" individual in a population, e.g. how competition affects the mean sizes of coexisting species. It is expected that selection should lead to size divergence of competing species, since this will reduce competition. It is assumed that there is a connection between morphology and resource utilization, such that size differences indicate niche differences. This has been shown to be the case in some studies on birds (e.g. Hespenheide 1971, Norberg 1979, Leisler 1980), lizards (e.g. Schoener and Gorman 1968), molluscs (e.g. Fenchel 1975) and insects (e.g. Pearson and Mury 1979). Thus, there is some support for drawing ecological inferences from morphological (characters related to foraging) data.

Competition does not only affect mean sizes and niche positions (average resource use, e.g. mean food size) of coexisting species. It can also affect the phenotypic variation and the niche width of a population, i.e. the range of resources that a population exploits. The primary aim with the present thesis has been to investigate the relationship between competition, both among and within species, for limited resources and the pattern of niche utilization and morphological variation within species.

Size differences between more or less genetically isolated bird populations occupying oceanic islands and nearby mainlands have been found in many species (see above). Such size differences may be due to differences in the competitive milieu and/or differences in the distribution and abundance of resources on islands and mainland. Besides such morphological differences between populations one can also imagine that individuals within a population, occupying different habitats, are of different sizes. If food abundance is greater in one place than in another, or if the average food particle size is larger, we may expect individuals of different sizes to be favoured in the different places or habitats. Also the number and size of competitors could have an effect on habitat selection. These problems were studied in a

population of willow warblers inhabiting small islands in a South Swedish lake and the nearby mainland (paper I). It was found that the individuals with territories on the mainland were larger than those on the islands. It was also found that food abundance was lower on the islands than on the mainland. The lower food abundance on the islands suggests that they represent a suboptimal habitat for the warblers. Therefore it can be assumed that mainland territories are preferred and that large individuals prevent smaller ones from establishing territories on the mainland. Thus, intraspecific competition can account for the correlation between habitat occupancy and warbler size.

As indicated above, individuals within a population may differ with respect to their resource exploitation and habitat utilization. Such differences are often reflected by the morphological variation within the population, since differences in morphological characters related to food-gathering often indicate differences in resource utilization (Schoener 1967, Roughgarden 1974, Grant et al. 1976). The niche width of a population, i.e. the range of resources that a population exploits, is partly due to the differences between individuals in their resource utilization and partly due to the variability of resources utilized by each individual. The extent of the segregation between individuals with respect to their resource use, and thereby the width of a population's niche is influenced by both intra- and interspecific competition. Intraspecific competition selects for increased segregation whereas interspecific competition tends to compress the niche of a population. The reason for this is that interspecific competition restricts the range of resources available for each competing species. Hence, a reduction of the number of competing species will lead to an increase of the variety of resources available for the remaining species. There is then an opportunity for deviating phenotypes to utilize unexploited resources. Compared to the predominating phenotypes in a population they will suffer less from intraspecific competition and will therefore have a selective advantage. As a consequence the phenotypic (morphological and/or behavioural) variation within the population will eventually increase. How is this increased variation realized? The form that such an increased variation is expected to take in a territorial species is discussed in paper II. Since territoriality will result in exploitative competition particularly between the male and the female in a pair, it is

concluded that the variation should take the form of sexual dimorphism. Increased niche separation between the sexes leads to a reduction of competition between the male and the female within a territory.

The predictions mentioned above were tested on two territorial bird species: the chaffinch (paper II) and the great tit (paper III). The habitat utilization of male and female chaffinches was studied on small islands in a South Swedish lake and the surrounding mainland. On the islands the number of potentially competing species ranged from 1 to 8 and on the mainland plot there were 26 potentially competing species. Thus, when going from the mainland to the islands, there is a very strong reduction in the number of competitors. On the islands, but not on the mainland, there were significant differences between the males and the females in habitat utilization. Thus, the predictions are consistent with the data.

Sexual size dimorphism in five morphological characters in the great tit was analyzed in three local populations inhabiting coniferous plantations (paper III). The plantations are surrounded by open cultivated land, in effect making them resemble islands. In the largest plantation the great tit coexisted with three competing congeners and in the two smaller plantations it coexisted with one congener. Concerning characters related to foraging (length, width and depth of bill, and tarsus length) there was a clear trend towards greater sexual size dimorphism in the plantations where the great tit coexisted with only one congener, while this was not true for wing length dimorphism. Thus, the prediction stating that phenotypic variation within a population should be greater under situations of relaxed interspecific competition is consistent with the observations. What is the adaptive value of this size dimorphism? Two hypotheses have been proposed to explain sexual size dimorphism. One, the sexual selection hypothesis, states that large size confers an advantage upon males in intrasexual competition for males. The other hypothesis, which is advanced in the present work, states that sexual size dimorphism is primarily an adaptation for ecological displacement between the sexes to reduce competition between them. The two hypothesis are not mutually exclusive. The former may explain differences in body size between the sexes, while the latter may be the more appropriate explanation for trophic characters. However, if there is a genetic correlation between body

size and bill size, sexual selection for dimorphism in body size may lead to a correlated response in bill size that secondarily results in ecological displacement between the sexes, making it difficult to establish the primary cause of the dimorphism. In birds, wing length may be used as an indicator of body size (Hamilton 1961). Concerning the great tit sexual dimorphism in wing length does not change in parallel with that in the characters related to foraging. Thus, changes in bill and tarsus size dimorphism are not merely consequences of a change in body size dimorphism, as indicated by wing length. These observations support the hypothesis that sexual size dimorphism in trophic characters is primarily an adaptation to reduce competition between the sexes.

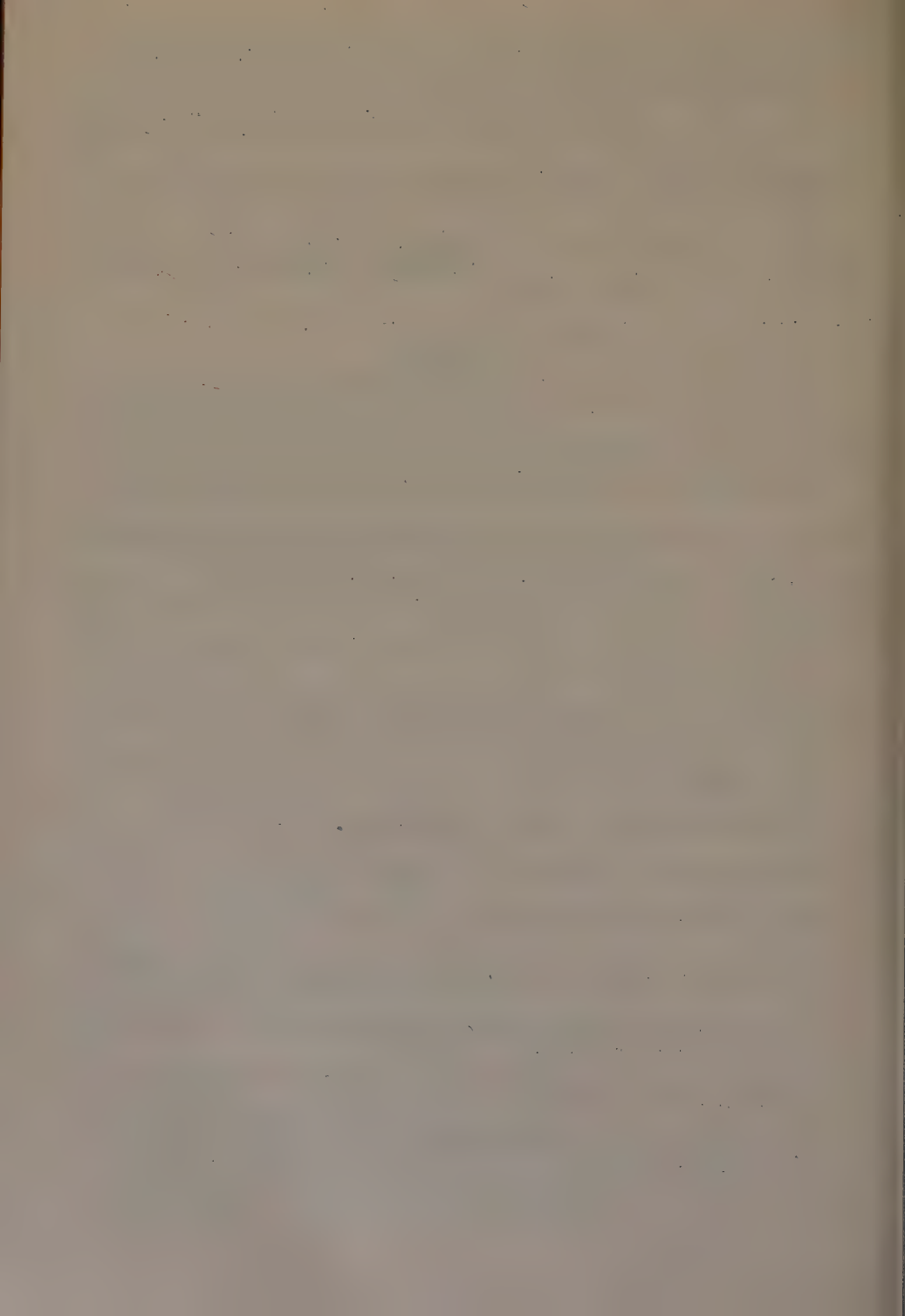
In the preceding sections the existence of niche differences between individuals in a population has been emphasized. However, there is still one component of a population's niche that hitherto has received practically no attention at all in niche theory: niche differences between individuals of different age. Many organisms (e.g. holometabolous insects, amphibians) have complex life cycles, undergoing metamorphosis during their postnatal ontogeny. A complex life cycle implies a complex niche, i.e. radical changes of the niche during postnatal ontogeny. Other organisms, like reptiles, do not undergo metamorphosis, but nevertheless they grow, some during their whole life. Since resource utilization is influenced by size, there are niche differences between the age classes also in these species. In paper IV I take a first step towards a formulation of a concept of the niche that takes differences in resource utilization between age classes in a population into account. Niche changes during postnatal development will affect both intra- and interspecific competition. An examination of how competition between age classes, as reflected by niche overlap, affects the stability of equilibrium abundances is undertaken. This is done in a discrete-time model for a population consisting of two age classes, where both reproduction and survival are frequency and density dependent. It is shown that increased competition sometimes has a stabilizing effect, in that it reduces the time lag effects inherent in the discrete-time model. This is contrary to conclusions reached by May et al. (1974) and Tschumy (1982). One reason for this is that they did not explicitly consider the mechanism of competition in their generalized models.

The equilibrium age distribution that is attained in a population is a function of the parameters, e.g. the niche positions of the different age classes, in the model. However, these parameters are themselves subject to evolutionary modifications by natural selection. An analysis of the ecological conditions that select for different patterns of resource utilization during postnatal ontogeny may lead to new insights in niche theory and the theory of life history evolution.

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SIZE PATTERNS IN WILLOW WARBLERS *PHYLLOSCOPUS TROCHILUS*
ON ISLANDS IN A SOUTH SWEDISH LAKE
AND THE NEARBY MAINLAND

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Differences in size of birds occupying islands and nearby mainlands have been found recently in many species (e.g., Grant 1965, 1979, Abbott 1974, 1977). The island populations studied have probably been more or less genetically isolated from the mainland populations. In such situations morphological differences between island and mainland birds can be expected, perhaps due to genetic drift or different selection pressures. However, it is also possible that members of the same Mendelian population occur in different habitats depending, for example, on size (van Balen 1967, Fretwell 1972). If food abundance is greater in one place than in another, or if the average food particle size is larger, we may expect individuals of different sizes to be favoured in the different places or habitats. Also, if competition for food is important, the number and size of

competitors could have an effect, i.e., differently sized individuals will be favoured under different competitive situations. We examined these possibilities in a population of the Willow Warbler *Phylloscopus trochilus* which breeds on small islands in a lake with one to ten other small (< 100 g) breeding passerines. On the nearby mainland there are more than 20 other species breeding in a small area (Nilsson 1977).

STUDY AREA

Many small islands with similar vegetation occur in the central part of Lake Möckeln (56°26'N, 14°02'E) where this study was conducted (Fig. 1). Heights of the canopy trees



FIGURE 1. A Willow Warbler study area in Sweden. The mainland is hatched with the two studied plots crosshatched. The numbers indicate the number of territorial males found in 1978.

are similar on the mainland and on the larger islands (> 0.15 ha), usually 18–24 m (Nilsson & Nilsson 1978). On the smallest islands, where no Willow Warblers were found, the canopy reaches 12 to 17 m and the shrub and tree vegetation is slightly denser than on larger islands. Generally vegetation density is similar on the islands and on the mainland (Nilsson 1977).

METHODS

We caught and measured 19 out of 21 Willow Warbler males present on the islands in 1978. In the same period, May to June, we measured 18 Willow Warbler males on the mainland near the lake. All warblers caught were males since they sang intensively when we played back the song. We recorded length, width and depth of bill, tarsus length, wing length and weight.

The abundance of insects (which constitute the food of the Willow Warbler (Haftorn 1971, Laursen 1978)) was estimated by placing 12 × 20 cm plates covered with tangle-foot at 0.1, 2 and 7 m in deciduous trees. Detailed description of sampling periods, number of plates put up, island sizes etc. is given elsewhere (Nilsson & Ebenman 1981).

RESULTS

The morphological measures were mostly inter-correlated and 12 out of 15 correlations were positive (Table 1). This is more than expected by chance ($P < 0.02$; Binomial test, one-tailed). The bill and weight measurements indicated that the island Willow Warblers were about 5% smaller than the mainland birds (Table 2). The wing length was only

TABLE 1

Product-moment correlation matrix between morphological characters of all the Willow Warblers measured

Variable	A	B	C	D	E	F
Length of bill (mm), A	1					
Width of bill (mm), B	0.31	1				
Depth of bill (mm), C	0.12	0.23	1			
Tarsus length (mm), D	-0.28	0.01	-0.22	1		
Wing length (mm), E	0.24	0.36	0.13	0.18	1	
Weight (g), F	0.10	0.14	0.17	-0.13	0.10	1

1.5% shorter and there were no differences in tarsus length. A statistical analysis revealed that the weights were significantly lower on the islands than on the mainland (Students *t*-test, two-tailed; $P = 0.007$). For bill length ($P = 0.10$), bill width ($P = 0.08$), bill depth ($P = 0.12$) and wing length ($P = 0.055$) the differences between mainland and island birds were nearly significant.

TABLE 2

Morphological measurements of island and mainland Willow Warblers. Arithmetic mean ± 1 s.d. is given

	Lengths of bill (mm)	Width of bill (mm)	Depth of bill (mm)	Tarsus length (mm)	Wing length (mm)	Weight (g)	n
Mainland	13.69 $\pm$ 0.79	4.28 $\pm$ 0.31	2.98 $\pm$ 0.29	21.58 $\pm$ 0.59	68.94 $\pm$ 1.63	9.81 $\pm$ 0.42	18
Islands	13.33 $\pm$ 0.45	4.01 $\pm$ 0.57	2.84 $\pm$ 0.22	21.60 $\pm$ 0.53	67.89 $\pm$ 1.57	9.35 $\pm$ 0.55	19
% Difference	-2.6	-6.3	-4.7	+0.1	-1.5	-4.7	—

Bill lengths were not correlated significantly (Kendall rank correlation test, two-tailed; $P = 0.15$) with island surface area. Taking the number of other small (< 100 g) bird species holding territories on the islands in 1976, instead of island area, the relation was statistically significant ($P = 0.011$). No statistically significant relation was found between any other measure and island size or number of other species. Although there was a non-significant tendency for wing length to be positively correlated with island area ($P = 0.12$), there was no such relation for weight ($P = 0.94$). If we combine the warblers from the islands and the ones from the two mainland plots where the number of potential competitors was assessed (Nilsson & Ebenman 1981) significant correlations between bird size and number of other species emerges. Warbler wing length correlates significantly with the number of other small bird species holding territories in the plots in 1976 (Fig. 2; Kendall rank correlation test, two-tailed; $P = 0.025$). A similar relation was found for bill length (Fig. 3; $P = 0.015$).

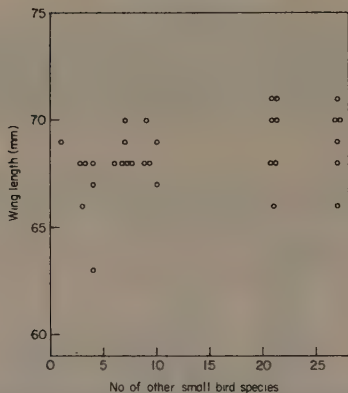


FIGURE 2. Relationship between wing length of Willow Warblers and the number of other small (<100 g) bird species holding territories in the plots.

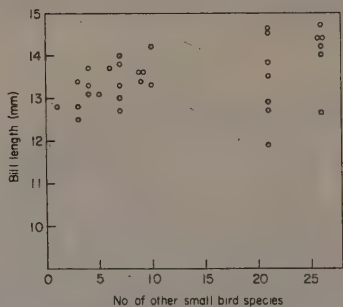


FIGURE 3. Relationship between bill length of Willow Warblers and the number of other small (<100 g) bird species holding territories in the plots.

Numbers of bird species probably reflect some other underlying factor which has more of a cause-effect relationship with bird size. This factor we believe to be food abundance. In Table 3 the abundance of arthropods in different size classes is given for mainland and islands. Obviously, the number of bird species in an area is related to available resources. Numbers of insects caught on the plates with tangle-foot, numbers of carabid beetles caught in pit-fall traps and proportion of leaves consumed primarily by Lepidoptera larvae are all positively correlated with number of bird species (Kendall rank correlation test, one-tailed test; $P = 0.015$, $P = 0.0014$ and $P = 0.0054$, respectively). Unfortunately, we cannot do a direct correlation analysis of bird size with food

TABLE 3

Average number of arthropods per station (three plates with tangle-foot) in relation to area and number of bird species breeding on islands and a mainland plot

Island area	Bird species (n)	Abundance of insects in different size classes (mm)					
		0-2	2-4	4-6	6-12	12	all
Mainland	25	153.2	77.8	63.5	21.6	12.3	328.5
0.97	9	88.3	64.6	62.0	13.6	6.7	235.4
1.04	9	50.1	46.3	61.6	23.7	27.5	209.3
0.29	4	44.5	79.0	18.0	14.5	6.0	162.0
0.08	2	76.0	40.5	29.0	42.0	2.5	190.0
0.13	1	64.0	58.0	20.0	27.5	1.5	171.0
0.03	0	29.0	31.0	14.0	3.0	1.0	81.0

abundance because we have too few islands where both birds were caught and food abundance assessed.

DISCUSSION

A vital assumption of our correlation analysis is that the number of species on an island is similar in different years. Ten islands were studied intensively both in 1976 and 1978. There was a close correlation between the number of territorial species on an island in the two years (Fig. 4).

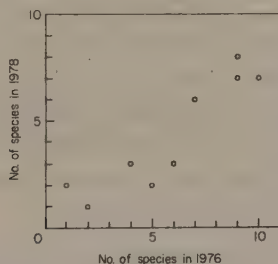


FIGURE 4. The correlation between the number of territorial bird species on islands in Lake Möckeln in 1976 and 1978.

Our results raise the question of whether Willow Warblers of different sizes select (or are forced to occupy) different territories depending on the occurrence of potential competitors or the food situation. As was mentioned above, the number of bird species in an area should obviously be related in some way to available resources (food abundance, food size, etc.). Therefore, it is difficult to separate the two hypotheses. It is even possible that both the food situation and the competitive milieu are causes behind the pattern we have found.

One possibility is that small Willow Warblers are more efficient than large ones at exploiting small insects. It is known that small animals on average eat smaller food particles than large ones (e.g., Hespeneide 1971). Then, if small insects were comparatively more common on the islands than on the mainland and more common on the

smaller than on the larger islands, small Willow Warblers could find the small islands more acceptable than large Willow Warblers. We know that the insect size pattern is the opposite to the one suggested in the above hypothesis (Table 3) and therefore, this explanation is not supported.

Optimal body size models developed by Schoener (1969) and Case (1978) predict that the optimum body size of an animal should be directly related to the availability of its resources. More precisely, all other things being equal, increase in food abundance will favour larger animals. Therefore, if food abundance is lower where there are fewer bird species, i.e., on the islands, we expect to find small birds there. Our data on the food situation (Table 3, Nilsson & Ebenman 1981) are consistent with this explanation. As was shown above, the density of insects is correlated with the number of bird species (see also Nilsson 1979). Roughgarden & Fuentes (1977) found that the average size of adult male *Anolis* lizards was strongly correlated with local insect abundance but not with average insect size.

Our finding that the biggest Willow Warblers occurred where potential competitors were most frequent suggests that large warblers may be more successful in inter-specific encounters. For example, the similarly sized Willow and Wood Warblers *Phylloscopus sibilatrix* seem to be inter-specifically territorial (Edington & Edington 1972). Since the Wood Warbler is slightly (about 10%) larger than the Willow Warbler, the former may on average be socially dominant (see Morse 1974). Perhaps the big but not the small, Willow Warblers can establish territories among the Wood Warblers that are common on the mainland but do not occur on the islands (Nilsson 1977). However, the Willow Warblers on the larger islands are bigger than those on the smaller islands, although there are no island Wood Warblers. This observation is not predicted from this hypothesis.

Both the comparatively much stronger decline of the Willow Warbler on the islands than on the mainland between 1976 and 1978 (Nilsson & Ebenman 1981), and the lower food abundance suggest that the islands represent a suboptimal habitat for the warblers. Therefore we may assume that mainland territories are preferred and that larger islands are preferred to smaller ones. A fourth possibility is that big Willow Warblers prevent smaller ones from establishing territories on the mainland, as large size may confer an advantage in competitive situations (Morse 1974). As shown above there is evidence that the mainland is more suitable than the islands. Therefore we expect the socially dominant Willow Warblers to settle on the mainland.

Summarizing, the available evidence supports the conclusion that both food abundance and competition (probably amongst the Willow Warblers themselves) can account for the correlation between habitat selection and warbler size.

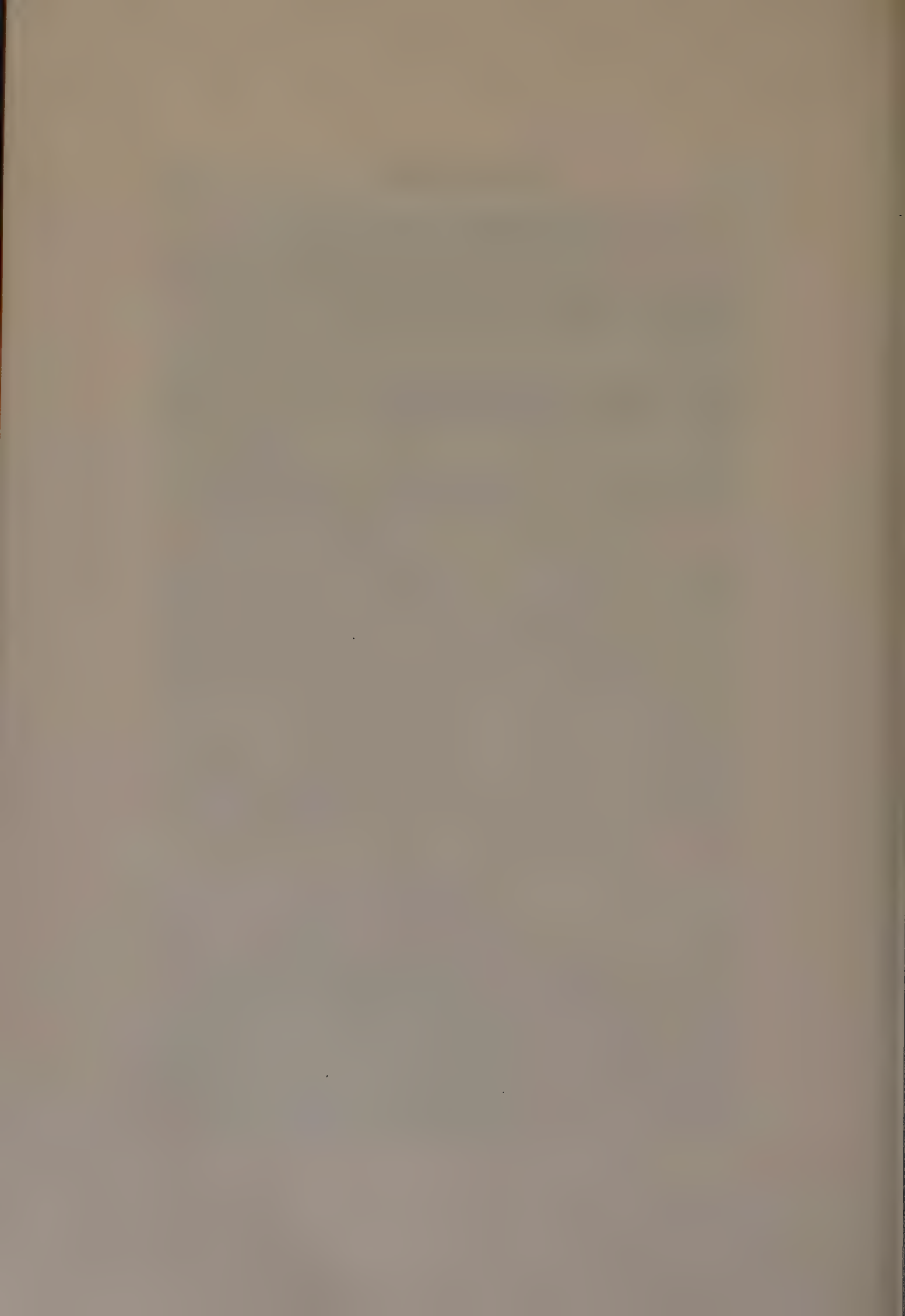
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COMPONENTS OF NICHE WIDTH IN A TERRITORIAL BIRD SPECIES:
HABITAT UTILIZATION IN MALES AND FEMALES OF THE
CHAFFINCH (*FRINGILLA COELEBS*) ON ISLANDS AND MAINLAND

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The niche width of a population, i.e., the range of resources that a population exploits, consists of two components. One, the within-phenotype component, reflects the variability of resources utilized by the average individual; the other, the between-phenotype component, reflects differences between individuals in their resource utilization. The sum of these two components is equal to the total niche width of the population (Roughgarden 1972, 1974). The between-phenotype component is related to the phenotypic variation within a population. Where competing species are absent we can imagine that extreme phenotypes can harvest unexploited resources. These extremes would then be selected for rather than against and this in turn will affect the niche width of the population as a whole. This is in accordance with Van Valen's (1965) niche-variation hypothesis which states that under conditions of relaxed interspecific competition an increased variety of resources available for specialization may permit greater phenotypic variation.

How is the increased phenotypic variation realized? Both continuous variation and different types of discontinuous variation, such as sexual dimorphism, increase the variation within a population. Clearly, we are most interested in the form of variation which increases the adaptive value of the members in the population. The kind of variation that will be adaptive depends to a large extent on the social structure of the species under study.

Here we will discuss variation within populations with reference to interspecific competition. We are especially interested in how the social structure of a population affects the form of variation that it will exhibit. We also present data from our own study, on the role of interspecific competition in molding the niche width and its components of a territorial bird species, the chaffinch (*Fringilla coelebs*). We analyze habitat utilization of males and females on small islands with few other bird species, and on plots on the surrounding mainland where the number of bird species is much higher.

INTERSPECIFIC COMPETITION AND THE PATTERN OF
VARIATION WITHIN POPULATIONS

Roughgarden (1974) showed how a population's niche width and its components (the between-phenotype component, BPC, and the within-phenotype component, WPC) are affected by interspecific competition and environmental productivity. Roughgarden predicted that along a gradient of decreasing number of competing species, but relatively fixed environmental productivity, BPC should increase. Hence, decreased interspecific competition leads to increased phenotypic variation within a population. The argument is that the variety of specialist phenotypes should be directly related to the variety of resources to specialize on, and as the number of competing species decrease the variety of resources available will increase. However, Roughgarden did not discuss what form this increased variation should take.

How will the social structure of a population affect the pattern of variability? Territorial species have social structures placing only paired males and females in exploitation competition with each other. For such species the pairs are spatially isolated from other members of the population. Since an individual is not engaged in exploitation competition with the rest of the members of its sex in the population, there is no need for variation within the sexes to reduce intraspecific competition. Considering a territorial species, we therefore do not expect selection for a general differentiation of the individuals within a population, as a result of a decrease in number of competing species. Instead we expect differences (morphological and/or behavioral) between individuals, i.e., males and females, within a territory. Thus, there will be selection for sexual dimorphism. This leads to a reduced level of intrapair competition which in turn allows for a smaller territory to satisfy a given energy demand. The smaller the territory is, the smaller are the energetic costs of defending and traveling, e.g., between feeding places and the nest. Habitat heterogeneity may cause variation within the sexes (ecotypic variation). However, in a given macrohabitat the different territories are expected to have similar structure and hence the optimal range of food types and foraging sites should be approximately the same for each member within a sex. Thus there is no reason to expect that males (females) occupying the different territories should differ in the set of food types and foraging sites utilized. Similar conclusions were reached by Hespeneide (1974) and Lister (1976*b*). For a given macrohabitat the within-phenotype component (WPC) should thus be approximately equal to the within-sex component (WSC) and the between-phenotype component (BPC) should be approximately equal to the between-sex component (BSC) of the population niche width (see discussion for further points).

At present, the data on resource partitioning within species are very limited, compared with data on the partitioning between species. These are primarily cases in which morphological differences between individuals, mostly males and females, in characters related to food-gathering indicate differences in resource utilization (birds: Selander 1966, 1972; Rothstein 1973; Hamilton and Johnston 1978; Grant 1979*b*; Newton 1979; lizards: Roughgarden 1974; Schoener 1977; and Lister 1976*a*, 1976*b*; fish: Feduccia and Slaughter 1974; ants: Davidson 1978;

Bernstein 1979). Some of these studies seem to support the hypothesis that decreased intensity of interspecific competition leads to increased variation within populations, especially in the form of sexual dimorphism. There are very few studies establishing a cause-effect relationship between interspecific competition and genetic variation within populations (Sabath 1974; Powell and Wistrand 1978; Johnson 1973).

Factors such as environmental heterogeneity, food availability, and gene flow can also affect intrapopulation variation and, therefore, must be observed carefully. Ideally, we want all factors except number of competing species to be constant. It is also important that comparisons be made on populations of the same species. Interspecific comparisons are less relevant when testing the hypothesis that variation within populations should be inversely related to number of competing species, because the number of adaptive peaks or opportunities for specialization may be different for different foraging modes irrespective of the number of competitors. Moreover, when studying the effect of interspecific competition on intrapopulation variation it is crucial that both sexes are represented in the sample analyzed.

A CASE STUDY

We have studied the resource utilization of male and female chaffinches (*Fringilla coelebs*) on mainland plots and nearby small islands, with respect to the habitat dimension. The mainland plots and islands differ in number of bird species and in average arthropod abundance. In the breeding season arthropods are the food for these birds (see Newton 1967, 1972).

Methods

Geographical area.—The field work was done on two mainland plots situated on promontories and on small islands (0.1–2.2 ha) in Lake Möckeln, southern Sweden. The distances between the islands in the lake and the surrounding mainland are at most about 1 km. The macrohabitat on the islands and mainland plots is essentially the same, dominated by deciduous trees. For detailed information see Nilsson (1977) and Nilsson and Nilsson (1978). The data were collected between May 16 and June 15, 1978.

Number of bird species.—The number of bird species and their densities were determined by the territory mapping method. One mainland plot and 10 islands were censused four to six times. Moreover, another mainland plot and 16 other islands were visited at least once. Censuses were also carried out at all these places during 10 visits in 1976 (Nilsson 1977).

Arthropod abundance.—The abundance of arthropods, chiefly insects, was estimated by the use of plates with a sticky, adhesive substance. The plates were put up at three heights (0.1, 2, and 7 m) in a tree. From May 16–24 there were seven such stations (trees) on the mainland and nine stations on the islands. From June 7–15 there were six stations on the mainland and 13 on the islands (Nilsson and Ebenman 1981). The arthropods were divided into size classes (0–2, 2.1–4,

4.1–6, 6.1–12, >12 mm) when analyzed. Also, the proportion of the leaves consumed by Lepidoptera larvae on the trees with the plates was estimated visually.

Habitat utilization.—The niche width for males and females was obtained by the distribution of the habitat utilization over habitat categories. The habitat was divided into five subdimensions which were divided into the following categories: (1) substratum subdimension (S): ground (G), coniferous tree (C), deciduous tree (D), air (A); (2) foraging height subdimension (H): the height at which the bird was foraging together with the height of the tree where foraging took place; (3) distance from trunk subdimension (horizontal position in tree, D): trunk (0), <0.5 m from trunk (1), 0.5–2 m from trunk (2), >2-m from trunk (3); (4) tree-part subdimension (TP): trunk (T); big branch (>30 mm Ø, BB); small branch (8–30 mm Ø, SB); twig (<8 mm Ø, Tw); leaves/needles (TwL); (5) foraging technique subdimension (T): gleaning (G), flycatcher-gleaning (bird in flight, FG), flycatching (bird and prey in flight, F).

Since some of these subdimensions are not continuous, it is not possible to calculate means and variances. However, partitioning of the population niche width into its two components (the within-sex component WSC and the between-sex component BSC) is also possible with discrete resource categories. The method and argumentation is taken from Roughgarden (1979, pp. 528–529). The measures of niche width are based on the Shannon information theory formula. Let X_h denote a resource category, and let Y_i denote a phenotype class (i = male, female). The original utilization data can be organized as a joint distribution function, $P(X_h, Y_i)$. This function is the probability that a unit of used resource is of type X_h and was used by phenotype Y_i . This function must satisfy $\sum_h \sum_i P(X_h, Y_i) = 1$.

From this function one defines two marginal distributions and two conditional distributions. One marginal distribution gives the population's phenotype distribution $p(Y_i)$, irrespective of their resource use: $p(Y_i) = \sum_h P(X_h, Y_i)$. The other marginal distribution gives the whole population's resource use, irrespective of what each phenotype utilizes: $u(X_h) = \sum_i P(X_h, Y_i)$. One conditional distribution represents the distribution of resource use for each given phenotype, $v(X_h | Y_i)$: $v(X_h | Y_i) = P(X_h, Y_i)/p(Y_i)$. The second conditional distribution represents the distribution of phenotypes that use any given resource, $\rho(Y_i | X_h)$: $\rho(Y_i | X_h) = P(X_h, Y_i)/u(X_h)$. The niche width for the total population is then calculated as

$$n^2 = -\sum_h u(X_h) \ln u(X_h).$$

The within-sex component is given by

$$WSC = \sum_i p(Y_i) \left[-\sum_h v(X_h | Y_i) \ln v(X_h | Y_i) \right].$$

The expression in brackets is the niche width of sex Y_i , and the WSC is the average of the niche widths of the two sexes. The between-sex component is given by

$$BSC = \left[-\sum_i p(Y_i) \ln p(Y_i) \right] - \left[\sum_h u(X_h) \left[-\sum_i \rho(Y_i | X_h) \ln \rho(Y_i | X_h) \right] \right].$$

The first term measures the evenness of the population's phenotype distribution among the phenotype classes. In this case the phenotype classes are represented by the sexes, which occur in equal numbers. "The second term measures the average evenness of the phenotype distribution, as 'seen' by the different resources. If the average phenotype distribution that encounters a resource is narrow, compared with the phenotype distribution in the population as a whole, then the different phenotypes must be using different resources" as explained by Roughgarden (1979, p. 529). The BSC is the measure of the extent to which the sexes use different resources. Finally, total niche width = BSC + WSC.

Each subdimension was treated separately. Using the χ^2 test for two independent samples we tested whether or not differences between males and females are significant. In order to meet the requirements of the test (not more than 20% of the cells with an expected frequency of less than 5) we combined adjacent categories. After this combination there were two categories left in each dimension (S: G, [A + C + D]; H: median test, D: [0 + 1 + 2], 3; TP: [T + BB + SB], [Tw + TwL]; and T: [G + FG], F).

Results

Number of bird species.—On the 10 islands visited four to six times the number of territorial passerine bird species ranged from 1 to 8. Combined bird population density ranged from 3.9 pairs/ha to 16.5 pairs/ha. (In 1976 the figures were 1–10 and 9.2–41.3, respectively.) On the mainland plot, which was censused five times, there were 26 territorial species and the combined bird population density was 10.5 pairs/ha. Thus, when going from the mainland to the islands, there is a very strong reduction in the number of bird species.

Arthropod abundance.—The average number of arthropods per station (3 plates) and the coefficient of variation on mainland and islands are shown in table 1. The variation in food abundance was greater on the islands in all size-classes except the smallest (0–2 mm). Generally, the smallest insects and spiders were most abundant, both on the mainland and on the islands. Abundance decreased with increasing size of insects and with increasing distance from the ground. In May, the abundance of insects and spiders on the islands was about one-third of that on the mainland where all size classes (0–2, 2.1–4, 4.1–6, 6.1–12 mm) were more abundant. In June, the abundance of small insects and spiders (< 4 mm) was again somewhat lower on the islands. However, the difference was not as marked as in May. The abundance of the larger sizes was approximately the same on islands and mainland. The proportion of leaves eaten by Lepidoptera larvae (which were also taken by the chaffinches) was approximately equal on islands and mainland.

In sum, the food abundance is somewhat lower on the islands than on the mainland. The reduction is not, however, very strong. For detailed information see Nilsson and Ebenman (1981).

Habitat utilization.—The niche widths (w^2) and their components (WSC and BSC) for the five subdimensions on the mainland (M) and the islands (I) are shown in table 2, and a computational example to illustrate the application of the Shannon information formula is shown in the Appendix. The proportions of the obser-

TABLE 1

THE AVERAGE NUMBER ($\bar{x}$) OF ARTHROPODS PER STATION (each with 3 plates in a tree)
AND THE COEFFICIENT OF VARIATION (C.V.) FOR MAINLAND AND ISLANDS
(data from May and June are lumped)

	SIZE CLASS (mm)				
	0-2	2.1-4	4.1-6	6.1-12	> 12
Mainland					
$\bar{x}$	76.9	38.0	32.0	11.1	12.3
C.V.	.72	.21	.64	.67	.54
Islands					
$\bar{x}$	35.1	31.3	21.3	12.5	7.7
C.V.	.52	.51	1.20	.73	.79

TABLE 2

NICHE WIDTH AND ITS COMPONENTS ON MAINLAND (M) AND ISLANDS (I)

	S	H	D	TP	T
$w^2_{\bar{x}}$ (51)	.93	1.87	1.13	.90	.87
WSC_M	.92	1.68	1.08	.75	.87
%	99	90	95	83	100
BSC_M	.01	.19	.05	.15	.0
%	1	10	5	17	0
$w^2_{\bar{x}}$ (83)	.86	1.88	1.10	.65	.80
WSC_I	.73	1.62	1.02	.58	.77
%	85	86	92	89	96
BSC_I	.13	.26	.08	.07	.03
%	15	14	8	11	4

NOTE.—Sample size shown in brackets. S = substratum, H = foraging height, D = distance from trunk, TP = tree-part, T = technique. w^2 = total niche width, WSC = within-sex component of the niche width, BSC = between-sex component of the niche width.

variations falling in the different habitat categories are shown in figures 1 to 5. It can be seen that the between-sex component (BSC) of the niche width is greater on the islands than on the mainland in four out of the five subdimensions. Thus, the overlap between the sexes in their habitat utilization is smaller on the islands than on the mainland. In the substrate dimension the females utilize the ground more than the males on the islands (χ^2 test, $P < .001$; fig. 1). In the foraging height dimension, the island males utilize the lower part of trees more than females which use the higher part more often (median test, $P < .01$; fig. 2). Concerning the distance from the trunk the island males mostly utilize the inner part of the canopy as opposed to females which more often use the outer parts (χ^2 test, $P < .01$; fig. 3). In the tree-part dimension (fig. 4), which is the only dimension where the BSC is smaller on the islands than on the mainland, there is no significant difference between males and females on the islands. In regard to foraging, island males more often catch their prey in flight than do the females (fig. 5), but the difference is not significant ($P < .20$).

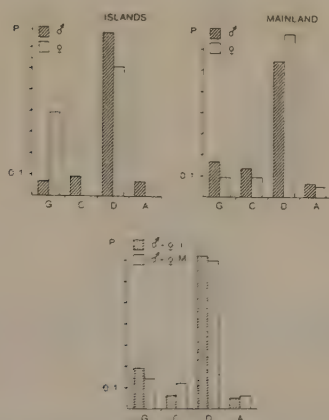


FIG. 1.—Proportions of observations of foraging birds falling in the different categories in the substratum subdimension (S): ground (G), coniferous tree (C), deciduous tree (D), air (A). The top diagrams are comparisons of males and females on islands and on mainland. The lower diagram is a comparison of the total island population ($\delta + \text{♀ I}$) and the total mainland population ($\delta + \text{♀ M}$).

There are no significant differences between males and females in any subdimension on the mainland. Moreover there are no significant differences between the total island population and the total mainland population in any subdimension.

DISCUSSION

Here we address the question of how interspecific competition will influence intrapopulation variation, especially with respect to resource utilization. Since there are other factors, such as environmental heterogeneity, gene flow, and food abundance that can also affect variation within populations, it is important to observe these factors. To test the influence of interspecific competition on population variation one should preferably compare situations where the number of competing species differ, but the other factors remain the same.

Grant (1979a, 1979b) found that there was greater variation in morphological characters within the sexes of chaffinch and blue tit in mainland populations than in populations from Atlantic islands. As Grant (1979b) points out, this is not surprising since environmental heterogeneity is probably more pronounced on the mainland; i.e., there may be more macrohabitats represented on the mainland, resulting in ecotypic variation. Moreover, mainland populations may be more open than island populations to gene flow from geographically differentiated

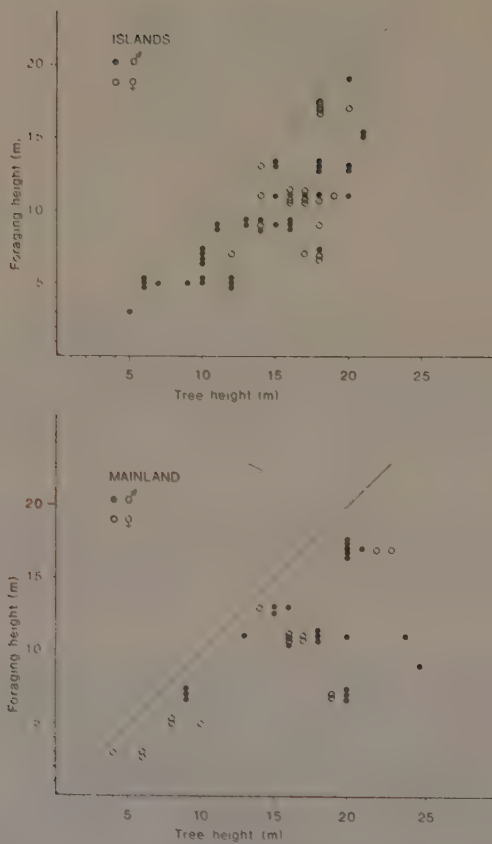


FIG. 2.—Comparison of the distributions of foraging of males and females on islands and on mainland in the foraging height subdimension (H). X-axis represents height of tree and Y-axis height of bird when foraging.

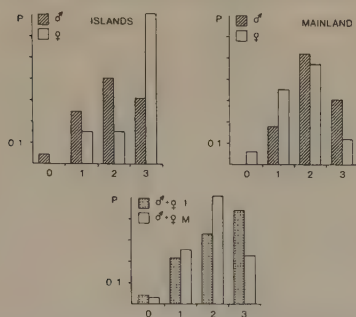


FIG. 3.—Horizontal position in trees of foraging birds. Proportions of observations of foraging birds falling in the different categories in the distance from trunk subdimension (D). Trunk (T), <0.5 m from trunk (1), 0.5–2 m from trunk (2), >2 m from trunk (3). For further information see legend of fig. 1.

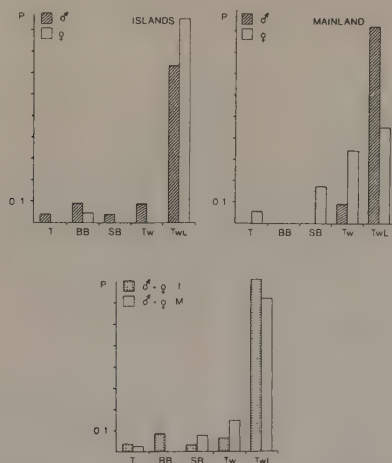


FIG. 4.—Proportions of observations of foraging birds in the different categories in the tree-part subdimension (TP). Trunk (T); big branch (>30 mm $\varnothing$, BB); small branch (8–30 mm $\varnothing$, SB); twig (<8 mm $\varnothing$, Tw); leaves/needles (TwL). For further information see legend of fig. 1.

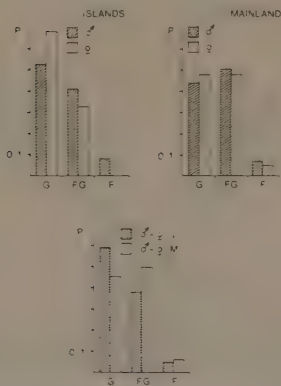


FIG. 5.—The utilization of different foraging techniques when catching prey. Proportions of observations falling in the different categories in the foraging technique subdimension (T). Gleaning (G), flycatcher-gleaning (bird in flight; FG), flycatching (bird and prey in flight; F). For further information see legend of fig. 1.

populations and this may lead to an increased variation within populations (Slatkin 1978). In our study there are no such problems. The environmental heterogeneity is essentially the same on the mainland plots and the islands. There is only one macrohabitat represented: deciduous forest (Nilsson 1977). Since the island and mainland birds belong to the same Mendelian population, gene flow will not affect the island and mainland birds differentially. Besides, the choice of where to search for food is probably only to a small extent genetically determined. Since the environmental heterogeneity and gene flow are the same for island and mainland birds, we do not expect these factors to be responsible for the different degree of sexual dimorphism in foraging behavior found between the island and mainland chaffinches. With respect to the same factors there is no reason to assume that variation in foraging behavior within the sexes will be different for island and mainland chaffinches.

The third factor, food abundance, does not remain the same when the mainland is compared with the islands. The average number of arthropods caught per station (3 plates) is lower on the islands (see table 1). This is especially marked for arthropods in the smallest size class (0–2 mm) where there is a 50% reduction. In the other size classes (2.1–4, 4.1–6, 6.1–12, > 12 mm) the abundance remains about the same when the mainland is compared with the islands (table 1). The proportion of leaves eaten by insects (primarily *Lepidoptera* larvae) was approximately the same on islands and mainland (about 10% and 9%, respectively). According to contingency models of foraging an overall decrease in environmental productivity should result in an increase in the variability of both food types and

habitat types utilized by an individual (i.e., WPC increases). A contingency model compares the energy per unit time gained from utilizing a resource unit (food types, habitat types) against that energy per unit time expected if the unit is skipped (Schoener 1971, 1974). An increase in the WPC leads to an increase in the overlap between the different phenotypes and, consequently, in the interphenotypic competition. This will, according to Roughgarden (1974), lead to a reduction of population variation, BPC, and total niche width. The explanation for this is that competition between individuals specializing in the center and the tails of the resource distribution increases, and since there are more individuals from the center the net effect will be to the disadvantage of individuals in the tails which will be selected against. However, this reasoning is not applicable in our case. We must make a modification concerning the relationship between BPC, total niche width, and interphenotypic competition. When there are just two phenotype classes, each of the same abundance (e.g., males and females), an increase in interphenotypic competition, which would result if WPC increases, should not necessarily lead to a decreased total niche width and BPC, although the BPC fraction decreases.

The reduction in food abundance (from mainland to islands) is, however, very slight compared to the reduction in number of competing species. The premises are then analogous to the ones in the prediction of Roughgarden (1974) which states that along a gradient of decreasing number of competing species, but comparatively fixed environmental productivity, the BPC (in this case BSC) should increase. This prediction is consistent with our data.

When studying the influence of interspecific competition on intrapopulation variation it is important to have an idea of the kind of variation that will be relevant. Both continuous variation and different forms of polymorphism increase variation within a population. The kind of variation that will be adaptive is among other things dependent on the social structure of the population under study. The chaffinch is a territorial species and we therefore expect intrapopulation variation to be in the form of sexual dimorphism. Thus both sexes must be analyzed with respect to their habitat utilization. If we had studied only males we could have drawn the incorrect conclusion that population variation remained the same in face of changes in the intensity of interspecific competition. For reasons outlined above, we do not expect selection for intrasex variation in a territorial species as long as we remain in one macrohabitat. Of course, to be sure that there are no differences within the sexes, one must analyze the habitat utilization of individuals. We have no data on this. The objection may be raised that even though the sexes as a whole have identical habitat utilization, the sexes within a given pair may nevertheless be different in their use of habitat types. Imagine two pairs, one in which the male forages in the height interval 1-5 m and the female in the interval 5-10 m and another pair in which the female utilizes the height interval 1-5 m and the male the interval 5-10 m. In spite of the fact that the sexes have identical height distributions when lumped together, the sexes within a given territory have nonoverlapping distributions. However, it seems unlikely that this pattern will be found in nature. We propose instead that for a territorial species within a given macrohabitat, the differences between the sexes within a

given territory will be proportional to the differences between the sexes as a whole.

Our study of the chaffinch deals only with the breeding season. Since the chaffinch is migratory and flocks during the winter, the selection pressures may be different during that time. This may complicate the picture for traits that are to a large degree genetically determined (e.g., morphological characters). When participating in flocks, there may be selection also toward differentiation within the sexes, especially if critical limitation of resources occurs during this time. However, even under these circumstances it may be problematic for intrasex variation to arise, especially for large and mobile animals like birds. Large size and great mobility will make the environment fine grained, precluding the occurrence of many adaptive peaks related to a subdivision of the niche. Levins (1968) has pointed out that when the fitness set becomes more convex, which is the case when size and mobility increase, there is decreasing probability that there will be selection for the evolution and maintenance of differentially adapted phenotypes (see also Selander and Kaufman 1973). In any case, the flock participation of chaffinches during winter should not disturb the picture in our study since foraging behavior probably is only to a small degree genetically programmed. It seems most likely that the differences we have documented between mainland and island chaffinches are brought about by behavioral plasticity. Hence, individuals can adapt to both summer and winter conditions by changing their behavior. Adaptations to winter conditions do not preclude adaptations to conditions that prevail during the breeding season. Although the differences between the sexes in their habitat utilization and the consequent increase of BSC on the islands is probably not a genetically programmed component of niche width, it is adaptive in that it reduces the competition between the sexes in a territory.

SUMMARY

Here we have discussed how interspecific competition will affect intrapopulation variation in traits (morphological and/or behavioral) involved in resource utilization. We concluded that decreased intensity of interspecific competition will lead to an increase in variation within a population. This increase in variation may be continuous or discontinuous (e.g., sexual dimorphism). For a territorial species within a given macrohabitat the increased variation is expected to take the form of sexual dimorphism. This prediction was tested by a comparison of the habitat utilization of the chaffinch, a territorial species, on small islands in a lake and the surrounding mainland. Both the number of potentially competing species and food (arthropod) abundance decreased from mainland to islands; there was a greater decrease in competitors than in food abundance. Components of niche width did show different patterns on the islands and the mainland; on the islands, but not on the mainland, there were significant differences between males and females in habitat utilization. Thus, on the islands, as compared to the mainland, the between-sex component of the population niche width was relatively large and the within-sex component relatively small. Sexual dimorphism entails an adaptive increase in variation within the population in that it reduces intrapair competition.

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APPENDIX

AN EXAMPLE OF CALCULATION OF TOTAL NICHE WIDTH, WSC AND BSC, FROM FIELD DATA USING THE SHANNON INFORMATION THEORY FORMULA

Phenotype Class Y_i	Frequency of Phenotype Class $p(Y_i)$	Foraging with Respect to Distance from Trunk (D). Proportions of Observations Falling in Different Categories $P(X_h Y_i)$			
		X_1	X_2	X_3	X_4
Y_{δ}	.5	.022	.122	.200	.156
Y_{ϕ}	.5	...	.075	.075	.350
The distribution of habitat utilization for the whole population $u(X_h)$	$u(X_h)$	.022	.197	.275	.506
	$\ln u(X_h)$	-3.817	-1.625	-1.291	-.681
The distribution of habitat utilization for each pheno- type $v(X_h Y_i)$	$v(X_h Y_i)$	.044	.244	.400	.311
	$\ln v(X_h Y_{\delta})$	-3.124	-1.411	-.916	-1.168
	$v(X_h Y_{\phi})$	...	.150	.150	.700
	$\ln v(X_h Y_{\phi})$	...	-1.897	-1.897	-.357
The distribution of pheno- types that utilize any given habitat category $\rho(Y_i X_h)$	$\rho(Y_i X_h)$		1.000	...	
	$\ln \rho(Y_{\delta} X_1)$		0	...	
	$\rho(Y_i X_2)$		.619	.381	
	$\ln \rho(Y_i X_2)$		-.480	-.965	
	$\rho(Y_i X_3)$		.727	.273	
	$\ln \rho(Y_i X_3)$		.319	-1.298	
	$\rho(Y_i X_4)$		.307	.693	
	$\ln \rho(Y_i X_4)$		-1.181	-.367	

$$\text{Total niche width} = -\sum_h u(X_h) \ln u(X_h) = 1.104$$

$$\text{WSC} = \sum_i p(Y_i) \left[-\sum_h v(X_h|Y_i) \ln v(X_h|Y_i) \right] = 1.015$$

Fraction WSC = 92%

$$\text{BSC} = \left[-\sum_i p(Y_i) \ln p(Y_i) \right] - \left[\sum_h u(X_h) \left[-\sum_i \rho(Y_i|X_h) \ln \rho(Y_i|X_h) \right] \right] = .089$$

Fraction BSC = 8%

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SEXUAL SIZE DIMORPHISM IN THE GREAT TIT (PARUS MAJOR)

IN RELATION TO THE NUMBER OF COEXISTING CONGENERS

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Sexual size dimorphism in five morphological characters in the great tit was analyzed in three local populations inhabiting coniferous plantations. In one plantation the great tit coexisted with three competing congeners and in the other two plantations it coexisted with one congener. Concerning characters related to food-gathering there was a clear trend towards greater sexual size dimorphism in the plantations where the great tit coexisted with only one congener, while this was not true for wing length dimorphism. It is argued that sexual size dimorphism in trophic characters is caused by natural selection for ecological displacement between the sexes to reduce competition between them, and that high intensity of interspecific competition greatly restricts the opportunity for evolution of sexual size dimorphism.

INTRODUCTION

The niche width of a population is partly due to within-phenotypic variation in resource utilization and partly to differences in resource utilization between phenotypes (Roughgarden 1972 and 1974). The between-phenotype component of the niche is sometimes related to the morphological variation within the population, since differences in morphological characters related to food-gathering often indicate differences in resource utilization (Hespenheide 1973 and ref. therein).

If the niche structure of a population depends on its competitive milieu, we expect changes in the niche utilization and the pattern of variation in trophic characters (e.g. bill size) when the species composition changes. A reduction in the number of competing species will lead to an increase of the variety of resources available for the remaining species. There is then an opportunity for deviating phenotypes to utilize unexploited resources. Compared to the predominating phenotypes in a population they will suffer less from intraspecific competition. Thus, they will have a selective advantage over the predominating phenotypes, and as a consequence the phenotypic variation within the population will eventually increase. In a territorial species the increased variation is expected to take the form of sexual size dimorphism (Selander 1966, Ebenman and Nilsson 1982).

Already Darwin (1871, Part 2, pp. 39,40) noted that sexual dimorphism in morphological characters related to foraging can have ecological significance. He wrote that "certain differences between the sexes... apparently depend on differences in their habits of life" and referred to the differences in bill morphology between the males and females of two hummingbird species and the now extinct huia (*Neomorpha*). For later studies see Se-

lander (1966), Schoener (1967), Bock (1970), Grant (1979) and Weatherhead (1980). But Darwin also pointed out that the sexual dimorphism may have been initiated by sexual selection (see also Campbell 1972 and Searcy 1979).

In this paper I shall discuss sexual dimorphism in five morphological characters in the great tit (*Parus major*) in relation to interspecific competition. The dimorphism was analyzed in three local populations inhabiting coniferous plantations of different sizes. It was found that the degree of sexual size dimorphism was dependent on the intensity of interspecific competition. Moreover, the findings support the hypothesis that sexual size dimorphism is an adaptation to reduce competition between the sexes.

METHODS AND STUDY SITES

The field work was done in three coniferous forest plantations in southernmost Sweden. The plantations differ as regards area (Fig. 1) but structural diversity and tree species composition are essentially the same. They are dominated by pine (*Pinus silvestris*)

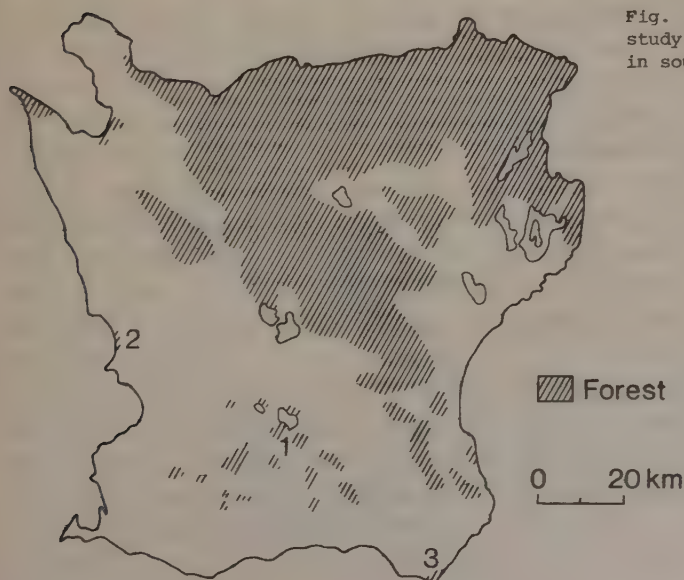


Fig. 1. Position of the study sites (1, 2, 3) in southernmost Sweden.

TABLE 1

Morphological measurements of male and female great tits. Arithmetic mean $\pm$ standard error and % difference between males and females are given. The statistical significance of the differences is also given (Students t-test; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

	Bill length (mm)	Bill width (mm)	Bill depth (mm)	Tarsus length (mm)	Wing length (mm)	n
Study site 1	♂	13.19 $\pm$ 0.08	4.44 $\pm$ 0.05	4.45 $\pm$ 0.02	18.91 $\pm$ 0.13	76.18 $\pm$ 0.42
	♀	13.05 $\pm$ 0.13	4.26 $\pm$ 0.08	4.29 $\pm$ 0.03	18.41 $\pm$ 0.23	72.70 $\pm$ 0.44
	% difference	1.06 n.s.	4.05 n.s.	3.60 ***	2.64 n.s.	4.57 ***
Study site 2	♂	13.23 $\pm$ 0.06	4.66 $\pm$ 0.03	4.56 $\pm$ 0.03	18.45 $\pm$ 0.10	76.94 $\pm$ 0.28
	♀	12.83 $\pm$ 0.08	4.52 $\pm$ 0.05	4.39 $\pm$ 0.03	17.89 $\pm$ 0.12	73.75 $\pm$ 0.27
	% difference	3.02 ***	3.00 *	3.73 ***	3.04 ***	4.15 ***
Study site 3	♂	13.30 $\pm$ 0.08	4.27 $\pm$ 0.05	4.35 $\pm$ 0.03	18.67 $\pm$ 0.15	75.67 $\pm$ 0.29
	♀	12.87 $\pm$ 0.14	4.03 $\pm$ 0.07	4.08 $\pm$ 0.02	17.68 $\pm$ 0.36	73.25 $\pm$ 0.28
	% difference	3.23 *	5.62 *	6.21 ***	5.30 **	3.20 ***

with some birches (*Betula* sp.) and oaks (*Quercus robur*) at the margins. The smaller plantations are more isolated from the main forest areas than the large one. The plantations are surrounded by open land, in effect making them resemble islands.

The largest plantation (study site 1) holds four breeding species of tits (*Parus major*, *P. ater*, *P. montanus* and *P. cristatus*) and the two smaller plantations (study sites 2 and 3) hold two (occasionally three) breeding species (*Parus major*, *P. ater*). The two missing species, *P. montanus* and *P. cristatus*, are extremely sedentary and their absence from the smaller plantations is probably due to area effects as explained by the theory of island biogeography (MacArthur and Wilson 1967).

Great tits were caught in the three study sites with the help of mistnets. Length, width and depth of the bill, tarsus length and wing length were measured with an accuracy of 0.05 mm on both males and females.

RESULTS

Table 1 gives the mean value $\pm$ standard error for bill length, bill width, bill depth, tarsus length and wing length in males and females, together with the difference between mean male and female measurements as a percentage of the mean male value. The statistical significance of the differences between the sexes was tested with the Students t-test. In the two plantations (sites 2 and 3) where the great tit coexisted with only one congener the differences between the sexes were statistically significant for all five characters. In study site 1, where there were four co-existing *Parus* species, the differences between the sexes were significant for only two of the five characters, viz. bill depth and wing length.

In Fig. 2 the differences between the sexes, for each character, for study sites 2 and 3 are compared to those for study site 1. There is a clear trend towards greater sexual size dimorphism in the localities with few congeners, the only exceptions being bill width (site 2) and wing length.

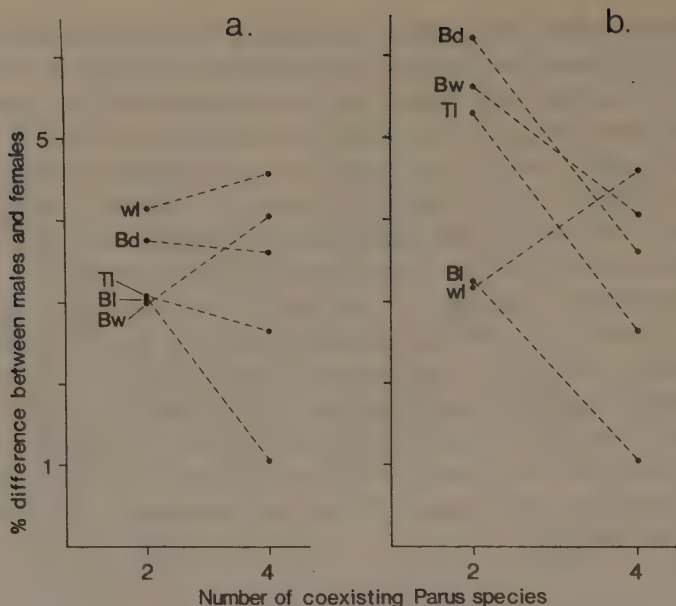


Fig. 2. The % difference between males and females of the great tit in relation to the number of coexisting congeners. a; study site 1 compared to study site 2 and b; site 1 compared to site 3. Bl = bill length, Bw = bill width, Bd = bill depth, Tl = tarsus length and Wl = wing length.

DISCUSSION

Interspecific competition restricts the range of resources available for each species in a community. Thus, when there is a reduction of the number of competing species, the variety of resources available for the remaining species will increase. It is then possible for the individuals in a population to segregate with respect to their resource use. Since the morphotype of an individual affects the types of resources that it exploits (Hespenheide 1966, 1971, Schoener and Gorman 1968, Grant et al. 1976), a reduction of the number of competing species might also lead to increased variation in morphological characters related to foraging. The form that such an increased variation is expected to take in a territorial species has been discussed by Ebenman and Nilsson (1982). Since territoriality will result in exploitative

competition particularly between the male and the female in a pair, it was concluded that the phenotypic variation should take the form of sexual size dimorphism. Increased sexual size dimorphism will lead to increased niche separation between the sexes, and hence to a reduction of competition between the male and the female within a territory. Lande (1980) pointed out that genetic correlation between the homologous characters of the sexes may greatly restrict the rate of evolution of sexual size dimorphism. It is well known from genetic experiments that selection on a character in one sex may cause a correlated response of the homologous character in the other sex (see Lande 1980 and ref. therein). However, Lande also pointed out that when genetic variation for sexual dimorphism is available, correlated selective responses between the sexes do not prevent the separate adaptation of each sex. Both sexes can then evolve to a locally optimal phenotype.

The great tit is a non-migratory species and is territorial in the breeding season and to a lesser degree so in the non-breeding season. As is shown in Fig. 2 the predictions mentioned above are consistent with the data. There is a clear trend towards greater differences in bill measures and tarsus length between the sexes in the localities where the great tit coexists with only one congener. Differences in these characters indicate differences in foraging. It has been shown that there is a correlation between bill length and mean food size in passerine birds (Hespenheide 1966, 1971). It has also been shown that the length of the tarsus is related to the manner of foraging. Birds which feed in a hanging position from thin twigs tend to have a shorter tarsus than birds foraging in an upright posture on thick perches (Grant 1965, 1971 and Fretwell 1969). The increased differences in bill and tarsus length between the sexes in the study sites with only one competing congener is mainly due to changes in the smaller sex, i.e. the females whose bills and tarsi become shorter. This is to be expected since the two absent congeners, the willow tit and the crested tit, both have shorter bills and tarsi than the great tit. In the study site where the great tit coexists with three competing congeners the opportunity for ecological displacement between the sexes is much smaller. Then, there is a greater need for ecological distinctiveness in the species as such to avoid competition with the other tit species. There are strong indications that these species really compete for resources in short supply,

at least during winter time (Ulfstrand 1976, 1977, Alatalo 1981, 1982, Ekman et al. 1981 and Jansson et al. 1981).

Two hypotheses have been proposed to explain the evolution of sexual size dimorphism. One, the sexual selection hypothesis, states that large size confers an advantage upon males in intra-sexual competition for mates. The other hypothesis, which is advanced in the present work, states that sexual size dimorphism is primarily an adaptation to reduce competition between males and females. The two hypotheses are not mutually exclusive. The former may explain differences in overall size between the sexes, while the latter may be the more appropriate explanation for characters related to food-gathering. The two hypotheses were put forward already by Darwin (1871) in his book on sexual selection. In discussing differences in the trophic niche between males and females of the goldfinch, Darwin wrote that "With a slight difference of this nature as a foundation, we can see how the beaks of the two sexes might be made to differ greatly through natural selection". But, he also pointed out "that the differences in the beaks may have been first acquired by the males in relation to their battles [sexual selection], and afterwards led to slightly changed habits of life [differential niche utilization]." Thus, if there is a genetic correlation between body size and bill size, sexual selection for dimorphism in body size may lead to a correlated response in bill size that secondarily results in ecological displacement between the sexes, making it difficult to establish the primary cause of the dimorphism. However, if a species only shows dimorphism in characters related to food-gathering (e.g. bill size) and not in body size, the most probable cause of the dimorphism is selection for ecological displacement between the sexes to reduce competition. This is the case in the huia and some woodpeckers (Selander and Giller 1963, Selander 1966). If there is no genetic correlation between the characters, they can change independently, in other words a change in bill size or tarsus size dimorphism is then not just a consequence of a change in body size dimorphism. Sexual selection and natural selection for ecological displacement between the sexes may then act simultaneously, the former on body size and the latter on bill size and tarsus size, without interfering with each other.

Concerning the great tit it can be seen from Fig. 2 that sexual dimorphism in wing length does not change in parallel with that in the other characters. In fact wing size dimorphism tends

to be more marked in the study site where the great tit coexists with three congeners. Thus, it can be concluded that the changes in bill size and tarsus size dimorphism are not just consequences of a change in body size dimorphism, as indicated by wing length. Hamilton (1961) and Van Balen (1967) have shown that wing length may be used as an indicator of body size. That bill and tarsus length do not change in parallel with wing length has also been shown by Grant (1965, 1968) in the context of character displacement between species. He found that bill length differences among homogenetic species were more frequently larger on islands than on the mainland, while this was not true for differences in body size, as indicated by wing length.

To conclude, the present work supports the hypothesis that sexual dimorphism in characters related to food-gathering is caused by natural selection for ecological displacement between the sexes to reduce competition between them. Moreover, the magnitude of the sexual size dimorphism is dependent on the number of coexisting congeners, being more pronounced in places with few competitors. This pattern cannot be explained as the result of competition in the past. More probably, competition is currently affecting the magnitude of the size differences between the sexes, since otherwise it would be expected that geneflow between the populations in the different plantations should have broken down the pattern.

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NICHE DIFFERENCES BETWEEN AGE CLASSES AND INTRASPECIFIC
COMPETITION IN AGE-STRUCTURED POPULATIONS

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A concept of the niche of a population that takes differences in resource utilization between age classes into account is developed. It is examined how competition between age classes, as reflected by niche overlap, affects the stability of equilibrium abundances. This is done in a discrete-time model for a population consisting of two age classes, where both reproduction and survival are frequency and density dependent. It is shown that increased competition sometimes has a stabilizing effect, in that it reduces the time lag effects inherent in the discrete-time model. Suggestions are also made on how to extend the theory to cover situations where birth and death processes occur continuously and where the niche position of an individual depends on its size.

INTRODUCTION

It is well known that many organisms have complex life cycles, undergoing metamorphosis during their ontogeny. (The fundamental meaning of ontogeny is the development of the individual, particularly the embryogenesis. In the present context it covers exclusively the postnatal development of the individual.) Examples are amphibians, holometabolous insects and many marine invertebrates. In fact the life stages of certain species are so different that not long ago the stages were believed, in some cases, to be different species. A complex life cycle implies a complex niche, i.e. radical changes of the niche during ontogeny. Other organisms, like reptiles and hemimetabolous insects, do not change that drastically during their postnatal development, but nevertheless they grow, some during their whole life. For example, young crocodilians become independent when they are only about 1/50 the weight of a sexually mature adult (see Bakker 1982). This results in populations consisting of many size classes. Since resource utilization is influenced by size there are niche differences between the age classes also in these species (Christian 1982, Mushingsky et al. 1982, Ross 1978, Schoener 1968).

Niche changes during ontogeny will affect intraspecific competition and hence population dynamics. Up to now niche theory has dealt exclusively with populations without age-structure. According to this theory (as developed by for example Roughgarden 1972, 1974) the niche width of a population consists of two components. One, the within-phenotype component, reflects the variability of resources utilized by the average individual; the other, the between-phenotype component, reflects differences between individuals in their resource utilization. The sum of

these two components is equal to the total niche width of the population. Christiansen and Fenchel (1977, p. 92) recognized that there is a third component, reflecting differences between individuals of different age in their resource utilization, but did not analyze its effect on intraspecific competition and population dynamics. As indicated above this component, which I will call the ontogenetic component, may make up a substantial part of a population's niche width. It is therefore important to include this component in competition and niche theory.

In this paper I will primarily analyze how competition between age classes, as reflected by niche overlap, affects population dynamics and stability of equilibrium abundances. This will be done in a discrete-time model for a population consisting of two age classes, by varying the ontogenetic component of the niche. I shall also make some suggestions on how to extend the theory to cover situations where the birth and death processes occur continuously and where the niche position of an individual depends on its size. When size determines resource utilization there is a continuous change of the niche position as the individual grows. Then competition between individuals of different age becomes a function of growth as given by the growth curve. A more detailed account of this is in preparation.

THE MODEL

The model to be investigated is a Leslie matrix with two age classes:

$$\begin{pmatrix} N_0(t+1) \\ N_1(t+1) \end{pmatrix} = \begin{pmatrix} m_0 & m_1 \\ s & 0 \end{pmatrix} \begin{pmatrix} N_0(t) \\ N_1(t) \end{pmatrix} \quad 1.$$

Here s is the fraction of individuals in age class 0 that survive to age class 1, m_0 and m_1 are the per capita birth rates for each age class. Survival and fertility are frequency and density dependent:

$$\begin{aligned} m_0 &= B_0 \exp [-k(N_0(t) + \alpha_{01}N_1(t))] \\ m_1 &= B_1 \exp [-k(N_1(t) + \alpha_{10}N_0(t))] \\ s &= S \exp [-k(N_0(t) + \alpha_{01}N_1(t))] \end{aligned} \quad 2.$$

B_0 and B_1 are the maximum per capita birth rates for each age class, S is the basic survival rate, k and k' are measures of the density dependent feedbacks on reproduction and survival respectively. k and k' are small when resource availability is high, going towards zero in the case of unlimited resource supply. The competition coefficient α_{01} measures the relative depression in m_0 and s , caused by an individual of age class 1 compared to another of age class 0. α_{10} measures the relative depression in m_1 , caused by an individual of age class 0 compared to one of age class 1. Assuming that $B_0=B_1=B$ and that competition is symmetric (i.e. $\alpha_{01}=\alpha_{10}=\alpha$) equation 1 can be rewritten to yield

$$\begin{pmatrix} \Delta N_0 \\ \Delta N_1 \end{pmatrix} = \begin{pmatrix} B \exp[-k(N_0 + \alpha N_1)] - 1 & B \exp[-k(N_1 + \alpha N_0)] \\ S \exp[-k'(N_0 + \alpha N_1)] & -1 \end{pmatrix} \begin{pmatrix} N_0 \\ N_1 \end{pmatrix} \quad 3.$$

The niche

Consider the case where competition between age classes is due to exploitative competition, and the limiting resources can be ordered along a resource axis. Overlap in resource utilization with respect to the resource axis is then an indication of competition. As explained by Roughgarden (1974), "the population's resource utilization function on the resource axis is the probably density function for resource use from different regions of the axis". The total niche width of the population with respect to the resource axis is then defined as the variance of the population's resource utilization function. The niche width of a population consists of three components: the within-phenotype component (WPC) which is due to variability in the resource use by each individual; the between-phenotype component (BPC) which is due to differences in resource utilization between individuals within an age class; and the ontogenetic component (OC) which is due to differences in resource utilization between individuals belonging to different age classes. These components can occur in different combinations. In the extreme case one of the components may contribute 100 percent to the total niche width of a population, while the others contribute nothing. In the following analysis the BPC is set to zero, meaning that there are no differences between individuals within an age class in their re-

source utilization. My main concern in this analysis is with differences in resource utilization due to age.

Let $v(x|a)$ be the resource utilization function of an individual belonging to age class a . Here x describes some resource quality that varies continuously, for instance prey size. The niche position of an individual belonging to age class a , D_a , is then defined as the mean of the utilization function $v(x|a)$

$$D_a = \int x v(x|a) dx \quad 4.$$

WPC can then be defined as the average variance of the individuals' utilization functions (Roughgarden 1974)

$$WPC = \overline{VAR[v(x|a)]} = \Sigma p(D_a) VAR[v(x|a)] \quad 5.$$

$p(D_a)$ is the frequency distribution of individuals with niche position D_a in the population. The ontogenetic component of the niche can then be defined as

$$OC = VAR[p(D_a)] \quad 6.$$

MacArthur and Levins (1967) proposed that the competition coefficients can be determined from the utilization functions with the following formula

$$\alpha_{ij} = \frac{\int v(x|i) v(x|j) dx}{\int v^2(x|i) dx} \quad 7.$$

Assuming that the resource utilization functions of age class i and j are normal-shaped and have the same variance, i.e.

$VAR(v(x|i)) = VAR(v(x|j)) = WPC$, it can be shown. (May 1974) that

$$\alpha = \exp(-d^2/4WPC) \quad 8.$$

where $d = |D_i - D_j|$ is the distance between the niche positions of the two age classes on the resource axis. The ontogenetic component is then a function of d . By varying d and inserting the resulting α values in equation 3. it is possible to analyze how changes in the ontogenetic component of the niche will affect population dynamics.

THE INFLUENCE OF NICHE DIFFERENCES BETWEEN AGE CLASSES ON POPULATION DYNAMICS

The zero growth isoclines of the two age classes are obtained by setting ΔN_0 and ΔN_1 in equation 3. equal to zero yielding

$$0 = N_0 \exp[-k(N_0 + \alpha N_1)] + N_1 \exp[-k(N_1 + \alpha N_0)] - N_0 \quad 9a.$$

$$0 = S \exp[-k'(N_0 + \alpha N_1)] - N_1 \quad 9b.$$

An equilibrium (N_0^*, N_1^*) satisfies the two equations simultaneously. This may be represented graphically by plotting the zero isoclines in the N_0, N_1 plane. An equilibrium point is then a point of intersection of the two isoclines. In figure 1 two examples of the zero isoclines and equilibrium densities are given; one where the distance between the niche positions of the two age classes is large and one where it is small. As expected the densities of the two age classes decrease when the niche overlap increases. It can be seen that the effect of increased competition is that the isocline of age class 0 bends towards the N_1 -axis and that of age class 1 towards the N_0 -axis. In this case the effect is strongest on the isocline of age class 0 because the density-dependent feedback on reproduction, k , is larger than that on survival, k' . The fraction of individuals of age class 0 will then decrease when competition increases.

Local stability of equilibrium points

Equation 3. can be written more generally as

$$\begin{pmatrix} \Delta N_0 \\ \Delta N_1 \end{pmatrix} = \begin{pmatrix} f(N_0, N_1) \\ g(N_0, N_1) \end{pmatrix} \quad 10.$$

An equilibrium point (N_0^*, N_1^*) satisfies

$$\begin{pmatrix} f(N_0^*, N_1^*) \\ g(N_0^*, N_1^*) \end{pmatrix} = 0 \quad 11.$$

Consider a small disturbance of the equilibrium point

$$n_0 = N_0 - N_0^* \quad 12a.$$

$$n_1 = N_1 - N_1^* \quad 12b.$$

Then

$$\begin{pmatrix} \Delta n_0 \\ \Delta n_1 \end{pmatrix} = \begin{pmatrix} \Delta N_0 \\ \Delta N_1 \end{pmatrix} = \begin{pmatrix} f(n_0 + N_0^*, n_1 + N_1^*) \\ g(n_0 + N_0^*, n_1 + N_1^*) \end{pmatrix} \quad 13.$$

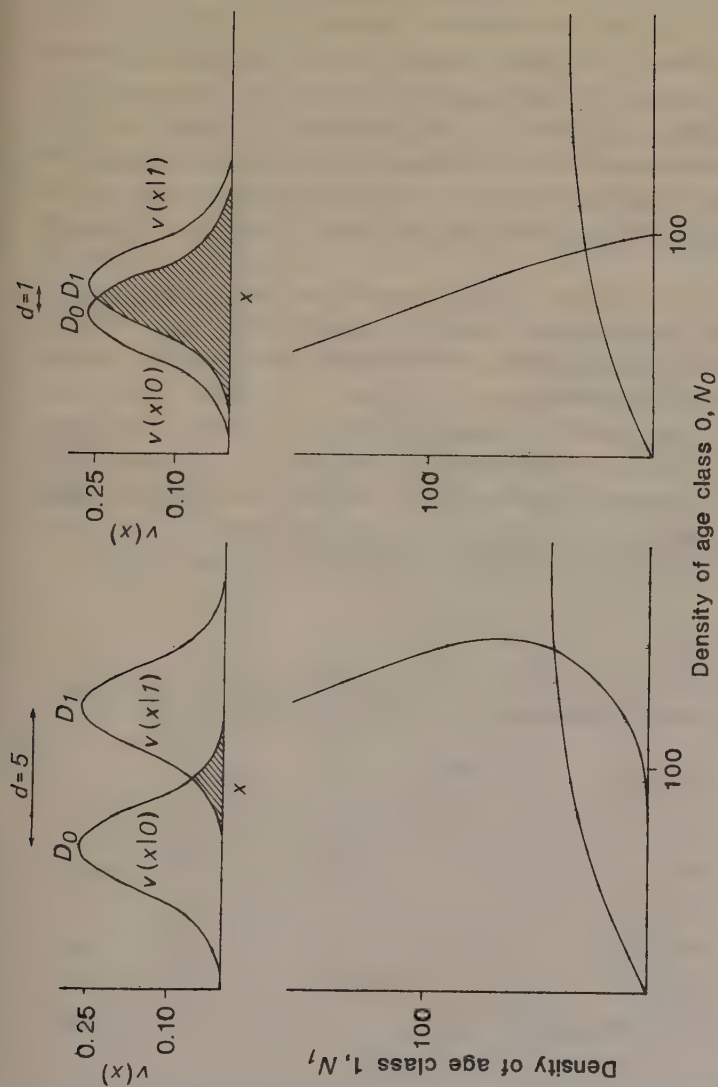


Fig. 1. Examples of niche utilization functions, $v(x|0)$ and $v(x|1)$, for the two age classes and the resulting zero isoclines and equilibrium densities. In case a, the distance, d , between the niche positions, D_0 and D_1 , of the age classes is large and in case b, it is small. $B = 4.5$, $S = 0.6$, $k = 0.015$ and $k' = 0.005$.

A Taylor series expansion of f and g about (N_0^*, N_1^*) yields

$$\begin{pmatrix} \Delta n_0 \\ \Delta n_1 \end{pmatrix} = \begin{pmatrix} \frac{\partial \Delta N_0}{\partial N_0} & \frac{\partial \Delta N_0}{\partial N_1} \\ \frac{\partial \Delta N_1}{\partial N_0} & \frac{\partial \Delta N_1}{\partial N_1} \end{pmatrix} \begin{pmatrix} n_0 \\ n_1 \end{pmatrix} \quad 14.$$

The partial derivatives in the Jacobian matrix describe the effect of small changes in the densities of the age classes upon ΔN_0 and ΔN_1 . Whether a given equilibrium point is locally stable or not can be determined by an examination of the eigenvalues, λ_1 and λ_2 , of the Jacobian matrix. More specifically, setting $\chi_i = \lambda_i + 1$ it is required that the roots χ_1 and χ_2 of the polynomial

$$\chi^2 + a_1\chi + a_2 = 0 \quad 15.$$

both lie within the unit circle in the complex plane centered at the origin (May 1973), where

$$a_1 = -[(\partial \Delta N_0 / \partial N_0 + 1) + (\partial \Delta N_1 / \partial N_1 + 1)] \quad 16a.$$

$$a_2 = [(\partial \Delta N_0 / \partial N_0 + 1)(\partial \Delta N_1 / \partial N_1 + 1) - (\partial \Delta N_0 / \partial N_1)(\partial \Delta N_1 / \partial N_0)] \quad 16b.$$

A necessary and sufficient condition for this to be the case is that

$$|a_1| < 1 + a_2 < 2 \quad 17.$$

(May et al. 1974). The elements in the Jacobian matrix corresponding to equation 3. are

$$\partial \Delta N_0 / \partial N_0 = m_0 + N_0^* \frac{\partial m_0}{\partial N_0} + N_1^* \frac{\partial m_1}{\partial N_0} - 1 \quad 18a.$$

$$\partial \Delta N_0 / \partial N_1 = N_0^* \frac{\partial m_0}{\partial N_1} + m_1 + N_1^* \frac{\partial m_1}{\partial N_1} \quad 18b.$$

$$\partial \Delta N_1 / \partial N_0 = s + N_0^* \frac{\partial s}{\partial N_0} \quad 18c.$$

$$\partial \Delta N_1 / \partial N_1 = N_0^* \frac{\partial s}{\partial N_1} - 1 \quad 18d.$$

where

$$\begin{aligned} \partial m_0 / \partial N_0 &\leq 0 & \partial m_1 / \partial N_0 &\leq 0 & \partial s / \partial N_0 &\leq 0 \\ \partial m_0 / \partial N_1 &\leq 0 & \partial m_1 / \partial N_1 &\leq 0 & \partial s / \partial N_1 &\leq 0 \end{aligned} \quad 19.$$

By inserting the partial derivatives into the condition 17. it can be determined whether an equilibrium point is locally stable or not. Levin and Udovic (1977) have pointed out that instability may arise either through time lags inherent in discrete-time models, or through properties of the interactions themselves (in this model the interactions between the two age classes). An equilibrium in a discrete-time system is intrinsically stable if the corresponding equilibrium in the analogous differential equation system (where there are no time lag effects) is stable. The condition for stability of the continuous-time analog of equation 3. is that $a_1 > 0$ and $a_2 > 0$ (the Routh-Hurwitz criterion, May 1973 b). Time lag effects may destabilize an intrinsically stable, discrete-time system.

I have examined how competition between the age classes affect stability, for some different birth rates and survival rates. It was found that increased competition sometimes has a stabilizing effect, in that it reduces the time lag effects. Three cases are illustrated in Fig. 2. In the first example the birth rate is low. The ratio between the response time of the system and the time delay is relatively large for low B's and this tends to stabilize the system (May 1973 b). Competition between the age classes has no effect on stability in this case.

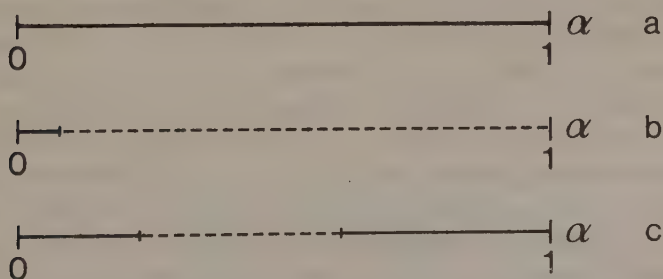


Fig. 2. Stability of equilibrium points as a function of the competition coefficient α . Solid line denotes stable and broken line unstable equilibrium points. In case a. $B = 3.32$, $S = 0.30$, $k = 0.012$ and $k' = 0.012$; in case b. $B = 11.0$, $S = 0.30$, $k = 0.024$ and $k' = 0.012$; in case c. $B = 11.0$, $S = 0.74$, $k = 0.024$ and $k' = 0.003$.

When the birth rate and the density dependent feedback on reproduction are increased the stability of the system becomes dependent on the intensity of competition. For low survival rates ($S=0.3$ and $k'=0.012$, second example) increased competition tends to destabilize the system. Fig. 2 shows that equilibrium points resulting from α 's greater than 0.08 are unstable. The instability is due to time lag effects. However, when survival is high ($S=0.72$ and $k'=0.003$, third example) increases in competition between the age classes may reduce the time lag effects and thereby stabilize the system. For example in case 3 Fig. 2, the equilibrium point that results from an α -value of 0.55 is unstable. If α is increased to 0.65 a new equilibrium point is attained which is stable.

The relation between the age classes can be characterized as a combination of symbiosis and competition. Destabilization of an equilibrium point cannot lead to the elimination of one of the age classes, since it will be recruited into the population in the next generation by the other age class. Destabilization leads to limit cycles or some other kind of bounded dynamical behaviour about the unstable equilibrium (see Guckenheimer et al. 1977).

DISCUSSION

May et al. (1974) and Tschumy (1982) have analyzed the effect of competition between age classes in a generalized discrete-time model with two age classes. In examining some special cases of competition between the age classes in their generalized model they found that strong interactions tend to destabilize a population's equilibrium. One purpose of the present work has been to expand the niche concept to cover populations with age structure where the niche position of an individual is dependent on its age. The present model is therefore more specified than the models of the authors above in that it incorporates the mechanism of competition, i.e. exploitative competition due to niche overlap. Tschumy analyzed the effect of competition between age classes on stability by varying the partial derivatives in the Jacobian matrix while holding the equilibrium densities constant. A change in the competition coefficient α , as defined in this work, does not necessarily lead to a parallel change in the partial derivatives in the Jacobian matrix of equation 14. This is because the

partial derivatives are evaluated at an equilibrium (N_0^*, N_1^*) , which itself is a function of α and hence of the distance between the niche positions of the two age classes. Tschumy did not explicitly consider α in his general model and was therefore not able to analyze its effect on population stability. An explicit consideration of α makes this possible, and as can be seen in Fig. 2 increased competition between the age classes may sometimes have a stabilizing effect.

In the present work it has been assumed that changes in the population density occurs in discrete steps. However, in many cases the birth and especially the death processes occur continuously. It has also been assumed that the niche position of an individual remains constant within an age class and then changes in one step as the individual enters the next age class. Now, consider the case where changes in the population density occur continuously. Moreover, assume that the niche position of an individual is determined by its size. This results in a continuous change of the niche position as the individual grows. The niche position during ontogeny is then determined by the pattern of growth as given by the parameters of an individual's growth curve. Thus, competition between individuals of different ages becomes a function of the pattern of postnatal development. A possible framework in which to analyze this problem is the transport equations introduced into biology by von Foerster (1959). VanSickle (1977) has generalized this model to cover individual traits, other than age, which change through time. Body size is such a trait. Let z denote the size of an individual, then

$$\frac{\partial n(z, t)}{\partial t} = - \frac{\partial}{\partial z} [f(z) \cdot n(z, t)] - \mu(z, [n(z, t)]) n(z, t) \quad 20.$$

$$B(t) = \int_{z_0}^{z_m} m(z, [n(z, t)]) n(z, t) dz$$

where $n(z, t)dz$ is the number of individuals in the size interval $[z, z+dz]$, $f(z)$ is the growth rate of an individual of size z . $f(z)n(z, t)$ is then the rate of passing of individuals through size z at time t , where $n(z, t)$ is the number of individuals of size z at time t . $\mu(z, [n(z, t)])$ is the death rate of an individual of size z . The death rate is also a function of the number and sizes of the other individuals in the population, which is

indicated by the term $[n(z,t)]$. $B(t)$ is the number of births at time t and is equal to $f(z_0)n(z_0,t)$ where z_0 is the size of newborn individuals and z_m is the maximum size. $m(z,[n(z,t)])$ is the fertility rate of an individual of size z and is also a function of the standing population $[n(z,t)]$. Once the functions $\mu(z,[n(z,t)])$ and $m(z,[n(z,t)])$ have been chosen equation 20. permits an analysis of the dynamics of a population with size structure that takes niche differences between the size classes into account. An analysis of this model is in preparation.

The equilibrium age distribution that is attained by a population, that can be modelled with the aid of equations like 3. and 20., is a function of the parameters in the model, especially of those that determine the growth pattern of the individuals (e.g. size of newborns, maximum size, growth rate). These determine the size and niche position during ontogeny and thereby the age-specific mortality- and fertility-schedules of the individuals in the population. However, these parameters are themselves subject to evolutionary modifications by natural selection. Since natural selection directly controls the parameters it also indirectly controls the population dynamics. Will selection set the parameters to values that result in stable or fluctuating populations? Will selection tend to modify the parameters in such a way that competition between age classes is minimized? An answer to these questions may be obtained by an analysis of a dynamic model that incorporates the genetic mechanisms of the evolutionary modification of the parameters in question (see Lande 1982).

A thorough theory of the niche that takes niche differences between age classes into account has not been developed yet, and as a consequence the effect of competition between age classes has not been incorporated into the theory of life history evolution. Since competition between age classes affects the age-specific mortality- and fertility-schedules of the individuals in a population it also influences life history evolution. For example, it has been proposed that synchronized reproduction in the periodical cicadas may be an adaptation to eliminate competition between the different age classes (see Charlesworth 1980). An analysis of the ecological conditions that select for different patterns of resource utilization during ontogeny may lead to new insights in niche theory and the theory of life history evolution.

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